PB82-223819

Acute Effects of Stream Acidification on the Diversity of Macroinvertebrate Drift

Cornell Univ.
Ithaca, NY

Prepared for

Environmental Research Lab.
Duluth, MN

Jun 82

U.S. Department of Commerce
National Technical Information Service

PB82-223819 EPA-600/D-82-289
Book Chapter

ACUTE EFFECTS OF STREAM ACIDIFICATION ON THE DIVERSITY OF MACROINVERTEBRATE DRIFT

by

J. Michael Pratt and Ronald J. Hall

Pages 77 - 95 in R. Singer (Ed.), Effects of Acidic Precipitation on Benthos. Proc. Symp. Acidic Precipitation on Benthos, 1980, North American Benthological Society. Hamilton, N.Y. Published 1981.

Copies of the entire Proceedings are available from:

Acidic Precipitation
North American Benthological Society
Box 878
Illinois Environmental Protection Agency
Springfield, Illinois 62705

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TECHNICAL REPORT DATA
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1. REPORT NO.	2.	3. RECIPIENT'S ACCESSION NO.
EPA-600/D-82-289	Book Chapter	PB82-223819

4. TITLE AND SUBTITLE	5. REPORT DATE
Acute Effects of Stream Acidification on the Diversity of Macroinvertebrate Drift	June 1982
	6. PERFORMING ORGANIZATION CODE
7. AUTHOR(S)	8. PERFORMING ORGANIZATION REPORT NO.
Pratt, J. M., and R. J. Hall	
9. PERFORMING ORGANIZATION NAME AND ADDRESS	10. PROGRAM ELEMENT NO.
Section of Ecology and Systematics Division of Biological Sciences Cornell University Ithaca, New York 14850	11. CONTRACT/GRANT NO.
12. SPONSORING AGENCY NAME AND ADDRESS	13. TYPE OF REPORT AND PERIOD COVERED
U.S. Environmental Protection Agency Environmental Research Laboratory-Duluth Duluth, Minnesota 55804	14. SPONSORING AGENCY CODE

15. SUPPLEMENTARY NOTES IN: R. Singer (ed.), Effects of Acidic Precipitation on Benthos, Proc. Symp. Acidic Precipitation on Benthos, 1980, North American Benthological Society, Hamilton, N.Y. (1981)

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Ecological implications of the acute changes in drift rate and diversity extrapolated throughout the low-order (1-3) tributaries of a weakly buffering stream are discussed. Recommendations for monitoring the effects of acid precipitation on the ecology of acid-sensitive lotic ecosystems are offered.

17. KEY WORDS AND DOCUMENT ANALYSIS

a. DESCRIPTORS	b. IDENTIFIERS/OPEN ENDED TERMS	c. COSATI Field/Group

18. DISTRIBUTION STATEMENT	19. SECURITY CLASS *(This Report)*	21. NO. OF PAGES
RELEASE TO PUBLIC	UNCLASSIFIED	20
	20. SECURITY CLASS *(This page)* UNCLASSIFIED	22. PRICE

EPA Form 2220-1 (Rev. 4-77) PREVIOUS EDITION IS OBSOLETE

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INTRODUCTION

Mounting evidence has strongly linked the deposition of acidic atmospheric pollutants to the gradual acidification of a growing number of lakes and streams in northern United States (Cogbill and Likens 1974, Galloway et al. 1976, Likens et al. 1979, Likens and Butler 1981). Moreover, several studies have implicated this acidification of surface waters by acid deposition as a major factor contributing to various deleterious changes in the ecology of poorly buffered freshwater ecosystems (Almer et al. 1974, Grahn et al. 1974, Beamish et al. 1977, Hendrey et al. 1977). The lakes and streams most affected by acidic rain and snow are located typically at higher elevations in northern latitudes where soils are poorly developed, acid-resistant bedrock predominates, and snow accumulates. Several investigators have reported that when an acid-contaminated snowpack thaws the initial meltwater can be very acidic (Leivestad and Muniz 1976, Schofield 1976). Consequently, a rapid late winter or early spring thaw could cause an abrupt and significant drop in the pH of lakes and streams in a watershed thickly blanketed by snow containing acid deposition. A sudden snowmelt,

therefore, may be a crucial event leading to acute hydrogen-ion stress for freshwater biota (Hall and Likens 1981).

Qualitative field surveys by biologists in Europe and eastern United States have shown that a direct relationship exists between high acidity at higher elevations and low diversity of aquatic invertebrates (Sutcliffe and Carrick 1973, Hendrey and Wright 1976, Fiance 1978). Most research to date on acidified lakes and streams, however, has collected relatively few quantitative data that describe changes in community structure, dynamics, and metabolism caused by hydrogen-ion stress alone. Yet such information is essential for predicting accurately and meaningfully what effects continued or intensified acid precipitation could have on the ecology of vulnerable freshwater ecosystems.

Hall et al. (1980) conducted a comprehensive study of various qualitative and quantitative changes in the biology and geochemistry of an experimentally acidified stream. A series of field experiments tested the general hypothesis that such acidification would alter stream chemistry and adversely affect the biota inhabiting Norris Brook, a small woodland mountain stream in the Hubbard Brook Experimental Forest, New Hampshire.

This particular paper focuses on the response of the macrobenthos in Norris Brook to hydrogen-ion stress as reflected by changes in the rate, diversity, and composition of macroinvertebrate drift. Monitoring drift may furnish useful data for describing and interpreting various ecological effects of acid deposition in streams because drift can influence the nutrient flux (Hall and Likens 1981), bioenergetics (Hall 1981), and community structure (Hall et al. 1980) of an acidified lotic ecosystem. Diversity is a parameter of biotic community structure commonly used to detect and assess the impact of environmental stress on the biology of freshwater ecosystems (Wilhm 1967, 1972, Wilhm and Dorris 1968, Cairns and Dickson 1971, Cairns et al. 1971). Other acid-induced changes in Norris Brook concerning water chemistry, insect emergence, macrobenthos, periphyton, and fish are presented elsewhere (Hall and Likens 1980a, 1980b, Hall et al. 1980).

STUDY AREA

The Norris Brook watershed occupies a south-facing slope with first- through third-order streams draining 87.2 ha (Fig. 1). The stream flows through a deciduous forest underlain by granitic bedrock and is subject to meterologic inputs of sulfuric and nitric acids at an annual volume-weighed pH near 4.0 (2.85-5.95 for individual storms).

The study area occupied a third-order reach of Norris Brook where mean width and depth were 1.8 and 0.2 m, respectively. The substrate varied in composition from fine sand to boulders 1 m in diameter. During the six-month study period (March-September 1977), water temperature ranged from 0.0-4.5°C in March to 11-20°C in July, but daily variation was only 2-3°C. Electrical conductivity varied from 21 to 30.5 µS, dissolved oxygen was near saturation throughout the study period, and ambient pH was usually between 5.4 (during storms) and 6.5.

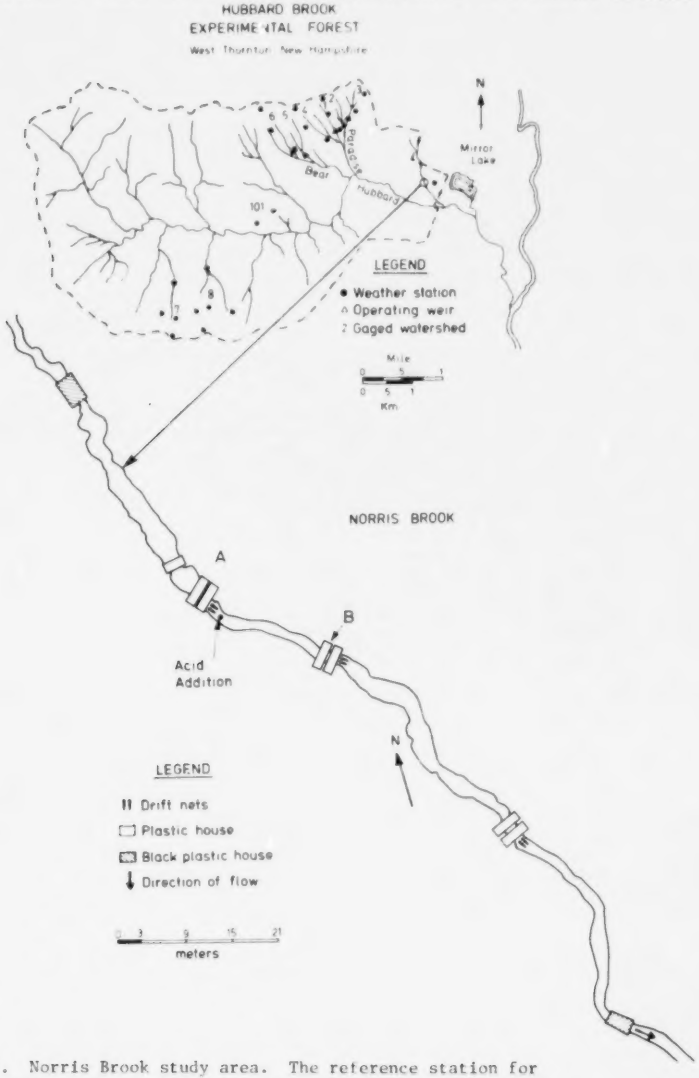

Fig. 1. Norris Brook study area. The reference station for drift sampling (site A) was 1 m above the acid addition point; the treatment sampling station (site B), 15 m below. The plastic houses collected insect emergence and the black plastic houses maintained constant light conditions for algal growth studies.

METHODS

Controlled dosing with dilute sulfuric acid (0.05-1 N) maintained an average pH of about 4 in the treatment or experimental portion of the study area. Acid addition began at 1200 h on 18 April 1977 and continued uninterrupted until 2400 h on 22 September 1977. Stream pH was measured routinely 5 m above and 12 m below the acid addition point with a Sargent-Welch Model PBL pH meter equipped with an A.H. Thomas glass electrode and a Fisher-Scientific Calomel electrode. Reference (control) and treatment sampling stations for drift were located, respectively, at sites 1 m above (A) and 15 m below (B) where acid was added (Fig. 1). The area of the intervening reach was 26.9 $m^2 \pm 0.6$. Stream pH was measured at short time intervals (e.g., every 5 minutes) when discharge changed rapidly during spates in order to maintain pH at 4 in the experimental section; but when discharge was relatively constant, pH readings were taken at least every 6-8 hours.

Drift nets upstream (site A) and downstream (site B) of the acid addition point sampled the macroinvertebrates moving into and out of the acidified reach. Each net was constructed of a weighted, polyvinyl chloride frame (15 x 30 cm) and an attached collecting bag of Nitex netting (mesh opening 253 µm). Two drift nets were anchored at midchannel at each site with wooden dowels driven through a board buried in the substrate (Waters 1962). Depth and current velocity was determined with a Marsh-McBirney 201 current meter.

Twenty-four hour drift samples were retrieved at 1200 h on the two days before (17 and 18 April) and on the first six days (19-24 April) of acid addition and then weekly until 22 September 1977. All drift samples, including plant debris and sediment, were preserved in 90% ethanol. The drift data presented here consist only of the two background samples from sites A and B and the first six treatment samples and their corresponding controls. The initial six days of elevated acidity simulated a pH regime that can occur in a small mountain stream during rapid snowmelt--an event hypothesized to have a major impact on the biota.

Drift samples were picked by hand, and the macroinvertebrates found were identified to the generic level except for chironomids (midges), which were keyed out to either Tanypodinae or all other subfamilies, mostly Orthocladiinae and Chironominae. Thus, these two groups of midges were treated as if they were two different genera because larval midges are generally either predators capable of swimming (tanypodines) or collectors that build fixed retreats or tubes (orthocladiines and other subfamilies); and, consequently, generic identifications would have provided little additional ecological differentiation of the functional roles or habits of individual larvae.

The census data (sample size, number of different genera found, and number of individuals/genus) of the two drift nets retrieved daily from a particular station were combined to yield a larger, more representative sample for determining drift diversity (Wilhm 1970). Generic diversity then was computed for each of the 16 pooled drift samples (eight from both A and B) using Brillouin's formula for diversity per individual (H) (Lloyd et al. 1968, Pielou 1975). Evenness (J) was also calculated to determine the equitability of abundance of the genera comprising each of the 16 drift samples (Hamilton 1975).

The decision to determine drift diversity at the generic rather than species level we feel is justified because the genus is thought to represent a valid ecological as well as a morphological type (Wiggins and Mackay 1978, Merritt and Cummins 1979). Thus, it was deemed sufficient to know what genus and associated taxonomic, trophic, and behavioral categories a macroinvertebrate belonged to in order to make generalizations about the response of macrobenthos to acute hydrogen-ion stress. Moreover, until more is known about the systematics and precise ecological requirements (e.g., food and microhabitat preferences) of many more macroinvertebrate species, calculating species diversity may not provide significantly more insight into community structure and function than that gleaned from generic diversity partitioned hierarchically.

Although diversity indices of various kinds condense and conveniently summarize large amounts of data, most can provide only an ecologically vague, quantitative basis for characterizing and comparing samples or organisms from biotic communities. This limitation occurs largely because diversity indices generally are unable to take into account and reflect qualitative or biological differences among organisms. Computing diversity alone furnishes, for example, little, if any, information about the phylogenetic affinities, trophic relationships, behavioral adaptations, life history strategies, and other potentially useful ecological data inherent in a sample. The Brillouin diversity index, however, does have the capacity to convey specific biological information, but this capability has been rarely exploited. The qualitative dimension of the Brillouin index comes into play if the organisms comprising a sample are classifiable in more than one way and when their diversity (e.g., at the species, generic, or some level) is partitioned hierarchically according to the classification scheme(s) chosen. Thus, it is possible to retain biological information that otherwise would be lost or wasted if the census data of a sample were simply condensed mathematically into a single diversity index.

We partitioned, therefore, the generic diversities of drift samples into three different sets of components, each representing a biologically meaningful way to classify macroinvertebrates above the generic level:

1. taxonomically (e.g., mayflies, stoneflies, caddisflies),
2. functionally according to feeding strategies (e.g., collector-gatherers, predators, filterers), and
3. behaviorally based on adaptations to a lotic habitat (e.g., clingers, swimmers, sprawlers).

Merritt and Cummins (1979) devised the functional and behavioral classification used. Equation (1) summarizes the first hierarchical partitioning of generic diversity:

$$H = H(GC) = H(C) + H_C(G) \qquad (1)$$

where H(GC) is the generic diversity of a sample, H(C) is the diversity among components (or component diversity) of a sample (e.g., diversity at the level of major macroinvertebrate taxa such as aquatic insect orders), and $H_C(G)$ is the mean within-component generic diversity averaged over all components. Equation (2) in turn dissects $H_C(G)$ into the generic diversities of the individual components comprising a particular classification:

$$H_C(G) = \sum_{j=1}^{c} (N_j/N) \cdot H_j(G)' \qquad (2)$$

where $H_j(G)'$ is the generic diversity of the jth component (e.g., mayflies) weighted in proportion to its contribution (N_j) to sample size (N). Pielou (1967, 1975) presents the derivation and more detailed formulations of equations (1) and (2).

RESULTS

Drift Rate

The similarity in size of the four background drift samples indicates that macroinvertebrates entered and left the treatment area at comparable rates (280-415/day) on each of the two days (days 1 and 2) before the experimental acidification period (days 3-8) (Fig. 2a). The drift samples at site A during the first and second days of acid addition (days 3 and 4) continued to move into the acidified reach at the background rate, but the drift sampled at B left at a much faster rate. On the second day of acid addition, for example, the drift rate at A (278/day) was only about one-tenth that at B (2739/day). The number of macroinvertebrates moving daily into the acid-stressed area declined from 278 to 181 over the next two days (days 5 and 6), but the number moving out decreased more than fivefold (from 2739 to 520). After another two days (days 7 and 8) of continuously acidic conditions (six days altogether), the drift rates at A and B were again comparable (~ 400-500/day).

The total number of macroinvertebrates drifting into and out of the treatment area, as inferred from the cumulative size of drift samples, increased at different rates during the experimental period (Fig. 2a). Ove the first three days of acid addition (days 3-5), the total number entering the treatment section increased at an average daily rate (326/day) less than one-fifth that (1745/day) of the total number leaving. Total drift at A increased on the average half as much (265/day) as it did at B (594/day) during the succeeding three days (days 6-8).

Generic Richness of Drift

The numbers of macroinvertebrate genera passing into and out of the treatment area before acid was added were nearly equal (at A 24 and 30 genera/day and at B 25 and 28 genera/day for days 1 and 2, respectively). The generic richness of reference drift gradually declined from 29 to 21 genera/day during the first five days of the experimental period (days 3-7), then peaked on the sixth day (31 genera/day) (Fig. 2b). Correspondingly, the number of genera drifting from the acidified reach increased from 28 to 41 per day for the first and second days (days 3 and 4) of acid addition before decreasing from 41 to 28 a day over the next four days (days 5-8). Reference drift during the first three days of stream acidification (days 3-5) collectively added eight new genera to the cumulative number of genera collected at A (Fig. 2b). The next three days of sampling (days 6-8) added another seven genera. Eight continuous days of drift sampling at the reference site yielded a total of 27 different benthic macroinvertebrate genera. Treatment samples for the first three days of acidification added 17 new genera to the cumulative number of genera collected at site B, while

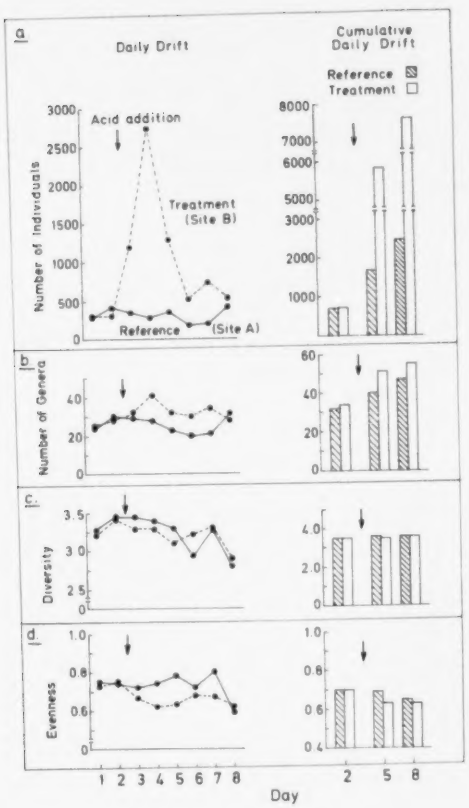

Fig. 2. The size (a), generic richness (b), generic diversity (c), and evenness (d) of daily and cumulative drift samples of benthic macroinvertebrates

collected from Norris Brook at sites A (reference) and B (treatment). The eight-day study period (16-24 April 1977) was divided into two days of background sampling (days 1 and 2) and six days of sampling during acid addition (days 3-8). Data plotted to describe cumulative drift are based on the pooled consus data of daily samples from each site collected over the first 2, 5, and 8 days of drift sampling. The heights of the vertical bars in Fig. 4a, for example, indicate the total numbers of macroinvertebrates collected by drift nets at A and B after 2, 5, and 8 days of continuous sampling. Vertical arrows indicate time of acid addition.

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the last three samples increased the count by only four. The eight daily drift samples from the treatment sampling site altogether contained 55 different genera. The dominant genera and chironomid subfamilies collected in drift nets at A and B are listed in Table 1.

Table 1. Dominant macroinvertebrates comprising the drift in Norris Brook sampled daily at sites A (reference) and B (treatment) from 16 to 24 April 1977. The eight-day study period consisted of two days of background sampling followed by six days of sampling during acid addition. The data tabulated are the percent contributions of various genera and subfamilies to cumulative drift collected after 2, 5, and 8 days of continuous sampling. Acid was added at the beginning of the third day of sampling.

Macroinvertebrate Taxa	Percent of Cumulative Drift					
	2 days		5 days		8 days	
	A	B	A	B	A	B
Ephemeroptera	25.3	27.3	25.7	50.8	23.0	42.8
Baetis	4.2	4.0	4.0	10.0	3.1	7.9
Epeorus	11.4	11.7	10.8	12.5	9.7	10.4
Ephemerella	6.0	8.9	7.1	20.0	6.7	16.7
Paraleptophlebia	0.4	0.7	0.7	2.7	0.8	2.6
Pseudocloenon	1.3	0.5	1.7	2.0	1.4	1.7
Diptera	38.6	40.0	41.6	35.8	47.2	40.6
Orthocladiinae & Chironominae	22.4	20.3	24.6	22.2	29.6	27.2
Prosimulium	13.5	15.7	13.4	9.1	13.2	8.3
Tanypodinae	2.2	3.0	2.6	2.8	2.9	3.1
Trichoptera	6.0	6.2	5.9	2.7	5.3	3.1
Hydroptila	1.4	1.5	1.3	0.7	1.1	0.7
Lepidostoma	1.9	1.6	2.0	0.7	2.0	0.9

Table 1 Continued.

Macroinvertebrate Taxa	Percent of Cumulative Drift					
	2 days		5 days		8 days	
	A	B	A	B	A	B
Rhyacophila	1.3	1.0	0.9	0.5	0.8	0.6
Wormaldia	0.7	1.2	1.0	0.5	0.8	0.5
Plecoptera	24.6	22.2	20.4	8.0	17.5	8.5
Isogenus	0.3	0.2	0.3	0.8	0.2	0.8
Leuctra	10.6	9.1	7.9	2.8	6.7	2.8
Peltoperla	0.5	0.2	0.7	0.2	0.9	0.4
Coleoptera	1.9	0.5	3.1	1.0	3.6	2.6
Oulimnius	1.6	0.5	2.8	0.9	3.2	2.2
Miscellaneous	3.6	3.6	3.3	1.7	3.4	2.5
Hydracarina	3.0	3.0	3.0	1.6	3.2	2.3
Total Percentage for Dominant Macrofauna	94.6	95.8	95.9	94.0	95.6	93.1

Generic Diversity of Drift

The generic diversities of background drift samples from sites A and B were comparable (H = 3.2-3.5). Drift entering the acidified reach was more diverse (H = 3.38) than that leaving (H = 3.23) for the first three days acid was added but less diverse (H = 3.01 vs 3.14) for the next three days (Fig. 2c). The differences in diversity between reference and treatment drift, however, were consistently small (<10%) compared to the corresponding differences in drift rates (187-921% greater at B than A). Similarly, the generic diversities of the cumulative drift at A and B were virtually equal (Fig. 2c).

Evenness of Drift

The evenness values of drift samples of macrofauna moving into and out of the treatment area were comparable before acid addition (J = 0.73-0.75). The evenness of reference drift sampled during the experimental period continued to remain within or near the background range until the sixth day of acid addition (day 8) when it decreased to its lowest value (J = 0.59) (Fig. 2d). Macroinvertebrate genera leaving the treatment reach throughout the first five days of elevated acidity were distributed less evenly (J = 0.62-0.68) among genera than those entering (J = 0.71-0.80) (Fig. 2d). By the sixth day of acid addition, however, the evenness of reference and treatment drift were almost equal again (0.59 vs 0.62) although still lower than background values. Finally cumulative reference drift was distributed more equitably among genera during the study period than was treatment drift, but this difference over the six-day experimental period (Fig. 2d).

Net Flux of Drift Diversity

Macroinvertebrates drifting into and out of the acidified reach were sampled to determine what effect stream acidification had on the transport of organisms, biomass, and nutrients in a lotic ecosystem. One method of analysis particularly appropriate for this research objective is estimating the net charge or net flux in drift, the difference between the drift leaving the acidified area at site B and the drift entering at site A. Although net flux in drift can be expressed in a variety of ways (e.g., as a change in numbers, biomass, or nutrient load), the parameter analyzed here is generic diversity and its taxonomic, functional, and behavioral components partitioned hierarchically to quantify biological differences distinguishing reference and treatment drift.

The net flux of generic drift diversity (diversity at B minus diversity at A) approached zero during the background sampling period, became negative for the first three days of experimental period, and then positive over the next three days (Fig. 3a). The daily values for net flux of diversity, however, were invariably small (i.e., 1-10% of reference diversity) during acid addition. Consequently, stream acidification did not appear to alter drift diversity to anywhere near the extent that it increased the drift rate (Fig. 2a).

Hierarchical partitioning of generic diversity into its taxonomic, functional, and behavioral components, however, reveals that the macrofauna abandoning the acidified reach was ecologically different from that entering from upstream. These qualitative differences were not evident from a quantitative comparison of generic diversities alone. Thus, analysis of the daily net flux of H(T), diversity among major taxa, reveals that the drift sampled on the two days before acid perturbation at site B was nearly as diverse taxonomically (i.e., at the level of major macroinvertebrate taxa) as well as generically as the drift sampled upstream at site A (Fig. 3b). These background drift samples from A and B were also comparably diverse at the levels of major functional (H(F)--Fig. 3c) and behavioral (H(B)--Fig. 3d) groups. For the first two days of acid addition, however, the net flux H(T) became increasingly negative indicating that macrofauna leaving the acidified section was markedly less diverse taxonomically than that entering. Drift at B relative to A also became noticeably less diverse functionally and behaviorally during this same period. Beginning on the third day of acidic conditions, drift from the treatment area steadily grew more diverse taxonomically. After the sixth day of continuous acid dosing, the drift vacating the treatment area was again about as diverse both taxonomically and behaviorally as that moving in. The functional diversity of the drift at B relative to that at A, however, had not returned completely to its background value (Fig. 3c).

Daily net flux of $H_C(G)$, mean generic diversity within components, generally varied inversely with H(C). Background net fluxes of mean generic diversity within taxa ($H_T(G)$--Fig. 3b), within functional groups ($H_F(G)$--Fig. 3c), and within behavioral groups ($H_B(G)$--Fig. 3d) usually were close to zero. Thus, the major taxa and the functional and behavioral groups leaving the treatment area prior to acid addition were on average as diverse generically as those entering. Through the first two days of elevated acidity, the net fluxes of $H_T(G)$, $H_F(G)$, and $H_B(G)$ became increasingly positive to varying degrees (Figs. 3b, c, and d). The major taxa and the functional and behavioral groups leaving the acidified

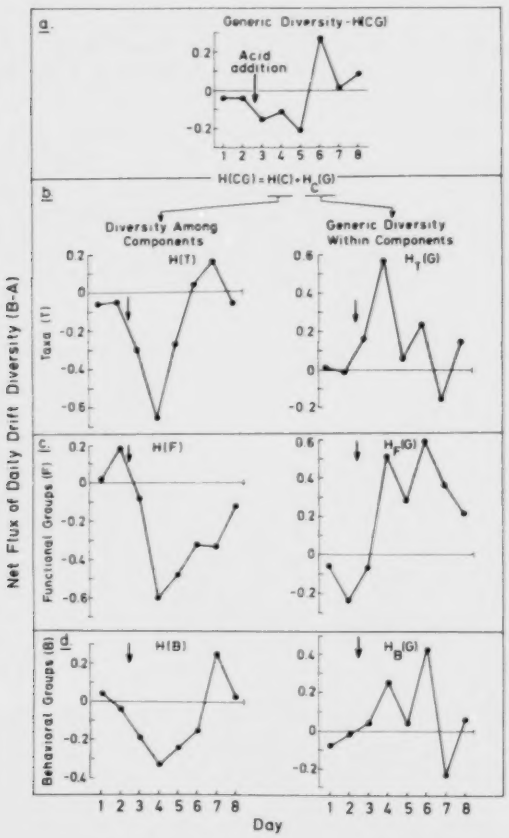

Fig. 3. Daily net fluxes of generic diversity H(CC) (a) partitioned into diversity among components (H(C) and mean generic diversity within components (H_C(G). The partitioning of diversity reflects macroinvertebrate classifications based on taxonomy (b), trophic function (c), and behavior (d). Net flux in diversity was positive, negative, or zero if drift diversity at B was, respectively, greater than, less than, or equal to drift diversity at A.

zone, therefore, were on average more diverse generically than those entering. For the next four days, the net fluxes of $H_T(G)$, and $H_B(G)$ tended to become less positive and approached their background levels. This downward trend denoted that the taxa, functional groups, and behavioral groups at B became less diverse generically relative to the drift at A.

Stream acidification appeared to have had little effect on drift diversity expressed solely as H(GC) (or H) because H(C) and $H_C(G)$ are additive (i.e., they sum to H(GC)) and because the net flux of H(C) and $H_C(G)$ usually varied inversely. Partitioning H(GC) taxonomically, functionally, and behaviorally, however, shows that major qualitative changes in macroinvertebrate drift had occurred under acidic conditions. The ecological significance of these changes can be further elucidated by subdividing $H_T(G)$, $H_F(G)$, and $H_B(G)$ into the respective generic diversities of individual taxonomic, functional, and behavioral groups (Fig. 4).

Partitioning $H_T(G)$ shows that the generic diversities of mayflies, true flies, caddisflies, stoneflies, and beetles comprising the background drift at A were comparable to the corresponding within-taxa diversities of background drift at B. Consequently, the daily net fluxes of the generic diversities of these insect orders were close to zero (Fig. 4a). The net flux of mayfly diversity became strongly positive in just two days of acid addition, while the net fluxes in the diversities of true flies, caddisflies, and stoneflies became negative to varying degrees. Net flux of beetle diversity remained at or near zero throughout the experimental period. Mayflies leaving the acidified reach, consequently, were initially more diverse generically than those entering. During the rest of the study period (days 5-8), this large early disparity between the mayfly diversities at A and B rapidly dwindled and eventually approximated background differences. True flies, caddisflies, and stoneflies drifting out of the treatment area on the first and second days of stream acidification became less diverse as groups generically than those drifting in. This decrease in the diversity of these taxa was reversed over the following four days, reestablishing background differences between the drift of A and B in terms of the generic diversities of true flies, caddisflies, and stoneflies.

Dissecting $H_F(G)$ into its subcomponents provides insight into hydrogen-ion induced changes in drift that is perhaps more valid and informative ecologically than that provided by a taxonomic breakdown of $H_T(G)$. The net flux of generic diversity for individual functional groups varied in magnitude during the study period and from one group to another. Background net fluxes of the diversities of collector-gatherers, predators, shredders, scrapers, and filterers fluctuated near zero and, thus, signified a functional equivalence of the drift entering and leaving the treatment area. From the second through the fourth day of acidic conditions (days 4-6), collector-gatherers abandoning the experimental reach were noticeably more diverse than those entering (Fig. 4b). Collector-gatherer diversity at B relative to A approached background levels on the next two days (days 7 and 8). Net flux of predator diversity continued to fluctuate near zero for the first three days of acidification but was slightly positive during the succeeding three days. In contrast, shredder diversity decreased somewhat at B compared to A for the first two days of elevated acidity but then increased throughout the following four days to its background value. Scraper diversity at B exceeded that at A on the first two days of acid addition, but the difference

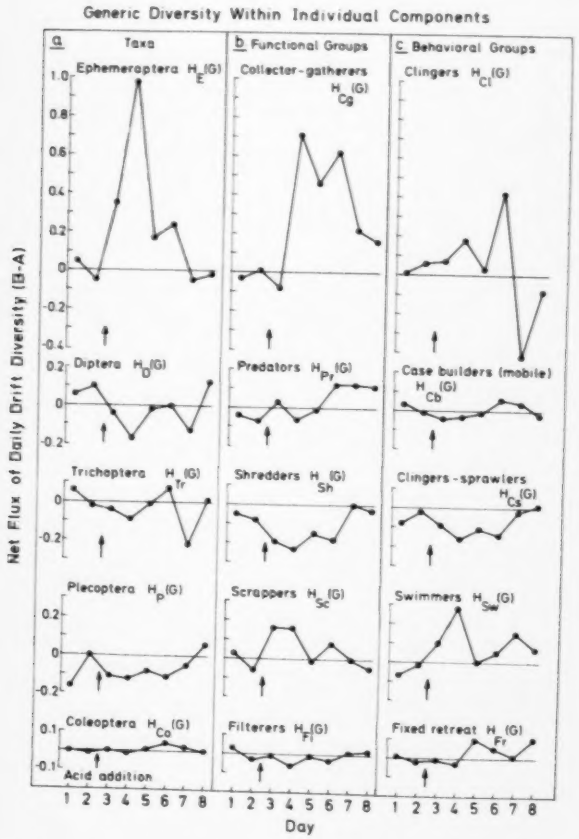

Fig. 4. Daily net fluxes of mean generic diversity within components partitioned into the generic diversities of individual taxonomic (a), function (b), and behavioral (c) groups. Net flux in diversity estimates the change, if any, in drift diversity at B relative to drift diversity at A.

declined to near zero over the next four days. The diversity of filterers at A and B were approximately equal during the entire experimental period.

The third and final partitioning of generic diversity involved a behavioral analysis of the drift entering and leaving the treatment area (Fig. 4c). Separating $H_B(C)$ into its constituent generic diversities produced a series of net fluxes that reflected differences in relative mobility among the behavioral categories found. Listed in order of decreasing vagility, these behavioral groups are swimmers, clingers and clinger-sprawlers, fixed-retreat dwellers, and case builders. The net flux in generic diversity for each of these groups was close to zero before acid was added, indicating a behavioral balance in the drift sampled at A and B (Fig. 4c). Swimmer diversity at B relative to A increased immediately after pH was lowered to 4, then returned to background levels on the third day of acidification. In contrast, the diversity of clingers at B compared to that at A did not increase appreciably until the fourth day of the experimental period. By the fifth day clingers vacating the treatment section were much less diverse than those drifting in from upstream. Clinger-sprawlers moving out of the acidified reach during the first four days of acid addition were slightly less diverse than those moving in, but the differences on the next two days were negligible. The drift diversities of case builders collected at A and B were similar throughout the experimental period. Finally, the difference in diversity for fixed-retreat dwellers drifting at A and B remained near zero for the initial two days of acid dosing, thereafter their diversity was slightly greater at B than at A.

DISCUSSION

The rapid mass exodus of benthic macroinvertebrates from the treatment area during the first two days of elevated acidity appears to have been an escape response to the acute stress caused by the experimental perturbation in stream pH. Moreover, this abandonment of the acidified reach by macrofauna occurred as a pulse in which the magnitude of the drift (sharply increased at first, then just as abruptly decreased. The macrobenthos in the acidified reach, therefore, presumably became substantially depleted in only 3-4 days of continuous acid addition because the initially high drift rates were temporary. From the seventh (25 April) through the 24th day (17 May) of continuous stream acidification, treatment drift slightly exceeded or equaled reference drift in density (Hall et al. 1980). Invertebrates entering the treatment zone, therefore, apparently did not recolonize the stream bottom while acid was still being added, otherwise treatment drift would have been less than reference drift in magnitude. This equilibrium in drift at A and B strongly suggests that macroinvertebrates drifting into the acidified zone continued on through to avoid the acute hydrogen-ion stress.

Seventeen genera and chironomid subfamilies out of the 55 collected accounted for at least 93% of the drift from the acidified reach (Table 1). The relatively large contribution of these 17 taxa to treatment drift can be attributed to a combination of their sensitivity to low pH (or associated changes in streamwater chemistry) and their relative abundance in the streambed. The uncommon genera collected at B (i.e., those found infrequently, if at all, in either background or reference samples) were responsible for augmenting the generic richness of treatment drift above that of reference drift. Even though richer in genera,

the drift leaving the acidified zone was slightly less diverse generically than that entering for the first three days of the experimental period and generally only negligibly more diverse during the next three days (Fig. 2). This apparent inconsistency is a mathematical consequence of the Brillouin diversity index, which combines the number of taxa (e.g., genera) in a collection and their frequencies of occurrence into a single numerical value. The macrofauna leaving the acidified reach, although richer generically, were distributed more inequitably among genera than were those entering. The tendency for more genera to increase diversity, therefore, was offset by a corresponding decrease in evenness. The net effect of this trade-off was a relatively small difference in diversity between reference (fewer genera but greater evenness) and treatment drift (more genera but lower evenness) throughout the experimental period.

A diversly index, such as H, that only takes into account the frequency distribution of organisms among taxa cannot adequately convey the underlying morphological, functional, and behavioral information differentiating one taxon from another. Thus, small quantitative differences in diversity may belie important and sizeable qualitative dissimilarities between or among samples of the same or different communities. Substantial decreases were observed, for example, in the taxonomic, functional, and behavioral diversities (H(T), H(F), and H(B)) of the drift abandoning the acidified reach relative to the drift entering (Figs. 3b, c, and d). Such reductions in diversity among components occurred because certain taxa and a few functional and behavioral groups dominated treatment drift more than reference drift. These disparities in relative abundance, which decreased evenness, and equality in the taxonomic, functional, and behavioral richness of the drift at A and B combined to lower all three H(C) values.

Greater mean generic diversities within taxa ($H_T(G)$) and within functional ($H_F(G)$) and behavioral ($H_B(G)$) groups at B relative to A tended to balance the corresponding decreases in H(T), H(F), and H(B) (Figs. 3b, c, and d). The increase in treatment $H_T(G)$ resulted primarily from the large number and high generic diversity of mayflies. Similarly, the increases in treatment $H_F(G)$ and $H_B(G)$ are due largely to collector-gatherers and scrapers and to swimmers and clingers, respectively. Chironomids also contributed heavily to the drift at B, and their generic richness is typically among the highest of the various macrobenthic groups found in pristine stream such as Norris Brook. Consequently, if chironomids had been identified to the generic level, Diptera (true flies) drifting from the experimental reach probably would have been more diverse generically than reported. The diversities of collector-gatherers and fixed-retreat dwellers, groups to which most chironomid larvae belong, perhaps would have been even higher at B than at A as well.

The rapid and large increase in drift rate during experimental acidification, particularly for mayflies and chironomids, and the accompanying increases in the drift diversity of mayflies and possibly chironomids strongly indicate that the macrobenthos inhabiting the treatment reach had been severely depleted in numbers and reduced in diversity. If extrapolated to the first- through third-order reaches of Norris Brok, such a depauperate and ecologically simplified macrobenthic community may provide an opportunity for acid-tolerant, fecund, or mobile species to fill the abandoned stream bottom physically and ecologically. Recolonization of the treatment area by at least one opportunistic species seems to have occurred since seven times more black fly larvae (Prosimulium) left the treatment area than entered during 16-17 November, two months after acid addition had ended (Hall, unpublished data).

The sizeable reduction in the collector-gatherer population inferred from its large and diverse exodus from the acidified reach may have important consequences concerning the fate of fine particulate organic matter (FPOM) in poorly buffered, low-order mountain streams stressed by acid deposition. Macrobenthic collectors (gatherers and filterers) play an important role in stream community dynamics and metabolism by ingesting, processing, and temporarily storing FPOM as it moves downstream (Wallace et al. 1977). Thus, if collectors are severely diminished in number and diversity by acidic snowmelt, a greater than normal proportion of FPOM and its associated nutrients and caloric content may be transported more rapidly and further downstream. A greater and more rapid export of FPOM from acid-stressed, low-order tributaries could affect, in turn, the structure and function of the macrobenthos further downstream (Cummins 1975).

The almost explosive escape response of macroinvertebrates from the treatment area during the first few days of acidic conditions could have serious consequences in the lower as well as upper reaches of a mountain stream subject to acid deposition. Acidified first- through third-order streams may have their capacities as a nursery for certain macroinvertebrate species and as a source of drift severely reduced. Downstream areas, therefore, may not receive an influx of invertebrates via drift at the normal time and in sufficient numbers, variety, or duration to replace individuals lost to predation, emergence, and drift. Furthermore, a short, intense melting of acidic snow is likely to induce the more mobile species (e.g., swimmers) to drift the furthest and, if repeated pulses of low pH occur, to disappear entirely from poorly buffered low-order streams. When these more mobile organisms resume their benthic existence in downstream areas where pH remains within a tolerable range, they may still continue to find conditions less than favorable for their survival and optimum growth (e.g., more intense predation by fish, greater competition for space and food, and warmer temperatures sooner in their life cycle). Less vagile species, in contrast, may suffer greater mortality or physiological injury by being incapable of escaping quickly from an acid-stressed reach.

Cairns et al. (1971, 1973) observed relatively rapid and complete recovery of macrobenthos subjected to hydrogen-ion stress. They attributed this quick and full recovery to the absence of residual toxicity from low pH and to abundant, diverse drift from unstressed upstream reaches and tributaries. If headwater and other low-order streams reach pH 4 during a snowmelt episode, however, drift probably would not be sufficiently abundant and diverse to initiate and sustain recovery of the macrobenthos. Recolonization of a streambed denuded during acidic snowmelt, therefore, would be more dependent upon the much slower aerial pathway leading to egg deposition by insects (Williams and Hynes 1976). This route to recovery also may be jeopardized if nearby streams and higher-order reaches become acidified.

Extrapolating the results of our experiment to Norris Brook as a whole begins to delineate and describe the potential harm that acid precipitation could cause in a poorly buffered, small mountain stream. Even a lowering of stream pH to 4.0 lasting only a few days, as could occur during a spring thaw, may have a serious long-term impact on the macrobenthos. Moreover, the direct ecological effects of acidification in low-order tributaries may have delayed secondary effects further downstream even though pH there remains above stressful levels (>5.6).

RECOMMENDATIONS FOR BIOLOGICAL MONITORING IN STREAM RECEIVING ACID DEPOSITION

Periodic drift sampling is an efficient and reliable way to detect and monitor ecological changes in small mountain streams vulnerable to hydrogen-ion stress. Benthic sampling (e.g., core sampling), in contrast, would probably be less effective in producing reliable, valid data since collecting bottom samples would disturb the benthos and, if routinely done, confound the effects of acid stress. Daily drift samples should be taken during snowmelt periods in late winter or early spring. Similarly, sampling before, during, and a few days after heavy rains would be appropriate for later in the year.

Data extracted from drift samples should include drift rates or densities and the number of each kind (e.g., genera) of macroinvertebrate collected. The organisms identified also should be sorted taxonomically, functionally, and behaviorally. If generic diversity is chosen as an additional descriptive variable, we strongly recommend that it be partitioned hierarchically to reflect and quantify ecological information such as trophic function. Both components of diversity, richness and evenness, also should be determined because they often vary independently of each other (Sager and Hasler 1969, Tramer 1969, Moore 1975) and, as a result, magnify or offset each other's contribution to diversity. Moreover, the results of our study show that the number of genera drifting and their evenness of abundance were each more responsive to acid perturbation than was generic diversity alone. This finding concurs with the observation that evenness is particularly sensitive to environmental stress (Tramer 1969).

We tentatively recommend mayflies and chironomids as indicators of acid precipitation in small mountain streams because these two groups exhibited the most noticeable response to experimental acidification in Norris Brook.

Monitoring programs designed and undertaken to detect and evaluate the various ecological effects of acid precipitation in lotic ecosystems should include collecting background data from low-order (1-3) mountain streams receiving little, if any, acidic deposition at present but vulnerable in the future. A representative sample of small, high-elevation stream suspected of having low pH because of acidic snowmelt or rain also should be monitored biologically to assess what ecological consequences, if any, ensue from an intensification of acid precipitation. Such a network of monitoring stations could function as an early warning system for signaling changes in surface water quality induced by acid deposition before such changes seriously endanger larger streams and lakes.

ACKNOWLEDGEMENTS

This study is a contribution to the Hubbard Brook Ecosystem Study. The National Science Foundation, the International Paper Company Foundation, and the United States Department of Agriculture, Forest Service, Broomall, Pennsylvania, furnished the facilities. We thank G. E. Likens for guidance and support during this study. We also acknowledge the technical assistance of B. Wesley and R. Haddock.

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